REMARKABLE FOSSIL FUNGI

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(WITH PLATES 180–182, CONTAINING 16 FIGURES)

Among the relics of former vegetation that carry the record back many millions of years the remains of fungi are so rarely found that their presence is always exceptional, although it is obvious that many times during the long history of the earth the environment has offered optimum conditions for their abundant development. To mention but one such occasion, that of the formation of the coal measures must have witnessed an exceedingly abundant mycological flora. That these plants were present thus early is indicated by the abundance of hyphae, and other traces of fungal activity such as butyric fermentation, in the tissues of Carboniferous vascular plants, and the scarcity of described forms must be attributed to the perishable nature of most fungal tissues and to the lack of systematic work by experienced mycologists on the more or less obscure material available. To be sure, quite a considerable number of fossil forms referred to Fungi have been recorded from various geologic horizons but the vast majority of these are leaf-spot types based upon real or fancied resemblances, and found on impressions of foliage and without definite botanical characters. Some undoubtedly represent fungal ravages, others are due to insects, some are glandular, and others are purely imaginary.[1]

Sometimes the traces of fungi preserved in petrified plant tissues are fortunately disclosed in sections and a number of well authenticated forms are known, principally from the Carboniferous, their discovery being due almost entirely to the relatively large amount of histological work that has been expended on the Carboniferous flora. Some of the more important of these will be mentioned in the following pages. The exceptional conditions of

[1] For a rather complete illustrated list of all of these forms down to the year 1900 the student is referred to Meschinelli, A., Fungorum Fossilium omnum Iconographia, 1902, 144 pp., 31 pls.

preservation afforded by the accumulations of amber at a time long subsequent to the Carboniferous have given us a glimpse of some few fungal types of the older Tertiary.

In the examination of a large series of petrified woods (the majority of which are of Tertiary age) for the United States Geological Survey, I have frequently noted the ravages of parasitic fungi as well as branching mycelia of both septate and non-septate hyphae. Most of these are too indefinite for incorporation in the record, but it may be safely concluded that fungi were obviously as abundant then as now, and among the remains discovered several are so exceptionally well preserved that their description becomes important to both the botanist and geologist.

The first of these may be called **Peronosporoides palmi** sp. nov., not so much because I am certain that it is related to the modern genus *Peronospora,* but because it resembles various living species in that genus and I believe is clearly referable to the Peronosporaceæ. It may be described as far as the nature of the material permits as follows:

Mycelium intercellular, freely branching, with fused cross branches. Hyphae thin, .0025 mm. to .00375 mm. in diameter, profusely septate, the lengths of the cells variable, no clamp connections observed. Oögonia intercellular, numerous, relatively large, spherical, terminal, about .0357 mm. in diameter. Antheridia somewhat smaller, about .0238 mm. in diameter, subspherical. Objects having all the appearance of oöspores or zoöspores are distinctly visible in some of the oöginia. *Pl. 180, f. 2,* shows two partially collapsed antheridia in conjugation with oögonia and the oögonia which are interpreted as containing oöspores are found in those oögonia as in *Pl. 180, f. 3,* where the antheridium is completely collapsed and only a trace of it is left or where it has entirely disappeared.

This form is exceedingly abundant and beautifully silicified in a small stem (about 7 cm. in diameter) of *Palmoxylon cellulosum* Knowlton from the lower Oligocene of Mississippi. Oögonia and antheridia are plentiful both in the broken down fibro-vascular bundles and in the intercellular spaces of the parenchymatous ground mass of the stem. Several of the oögonia show what are clearly to be interpreted as spores and after making a careful survey of the literature I feel justified in asserting that this is the

best preserved fungus thus far discovered. It is true that this Oligocene species is very similar to the type figures of *Peronosporites antiquaria* Worthington Smith[2] but his figures are evidently idealized from his knowledge of recent fungi, if reliance can be placed on Seward's statement[3] that "Prof. Williamson and others have carefully examined the specimens, but they have failed to detect any trace of reproductive cells enclosed in the spherical sacs." Whether this does or does not do an injustice to the original describer of *Peronosporites antiquarius* I am unable to state, but feel disposed to give full weight to Seward's statement since this form has been found to be quite abundant in the scalariform tissues of *Lepidodendron* and both Cash and Hick[4] and Williamson[5] have described similar material. The latter author states that an examination of Smith's type as well as additional slides failed to show any oöspores or any septation of the hyphae and he states that its botanical relations are with the Saprolegnieae and not with the Peronosporaceae.

A form very similar to the English species has been described from the French coal measures as *Palaeomyces* by Renault,[6] and Coulter and Land[7] have recently figured what appear to be antheridia and oögonia which they found in rootlets that had penetrated a *Lepidostrobus* cone from the Carboniferous of Warren County, Iowa. Jeffrey[8] has described and figured a fungus found in the Tertiary lignites of Brandon, Vermont, which he calls *Sclerotites brandonianus* and which while he interprets it as a sclerotium stage, is not unlike *Peronosporoides palmi,* although it occurs in dicotyledonous instead of monocotyledonous wood and is not nearly as well preserved as the latter species.

To avoid any possible errors of representation, I have therefore

[2] Gardeners Chronicle, vol. 8, 1877, p. 499.

[3] Fossil Plants, 1898, p. 218.

[4] Cash and Hick, On fossil fungi from the Lower Coal-Measures of Halifax. Proc. Yorkshire Geol. Polyt. Soc., vol. 7, 1878, p. 115.

[5] Williamson, W. C. Philos. Trans. Roy. Soc., vol. 172, 1881, p. 300, pl. 48, figs. 36–38; pl. 54, figs. 28–33.

[6] Bassin houiller et permien d'Autun et d'Epinac, Fasc. IV, 2e partie, 1896, pp. 439, 441, figs. 88, 89, 90.

[7] Coulter and Land, Bot. Gaz. vol. 51, 1911, p. 452, figs. 21–23.

[8] Jeffrey, E. C., Geol. Surv. Vermont, Rept. from 1905–1906, p. 200.

illustrated this species photographically, although drawings would bring out the details to better advantage. I have submitted specimens to the mycologists of the Bureau of Plant Industry and wish to record my indebtedness to Mrs. Flora W. Patterson, the Mycologist in Charge of the Pathological Collections, for information and suggestions. She has confirmed the presence of oöspores in some of the oögonia and was disposed to consider the form identical with *Peronosporites antiquarius*. In review of the statements of Murray (in the Academy, Nov. 17, 1877), and of Williamson and Seward mentioned above, it is obvious that we are dealing with a distinct form. Due weight must also be given to the enormous time interval between the Carboniferous and Oligocene, as well as the geographic interval between Yorkshire and Mississippi. Moreover the oögonia of the American species are more than twice the size of the supposed oögonia of *Peronosporites antiquarius*.

Regarding the botanical position of the present form it is clearly a Phycomycete and belongs to the group Oömycetes. In the latter group I cannot find any family of existing forms to which it can be referred other than the Peronosporaceae. It is, of course, necessary to consider whether the existing families extend back in time some million of years, and on this point I am inclined to think the endoparasitic forms have varied but little since they assumed their present mode of life in their substantially unchanged environment. The Peronosporaceae are commonly thought of as exclusively endoparasitic in leaves and as exserting their spore-producing apparatus into the air through stomata or dissolved cuticles, thus producing the familiar downy mildews. A number of forms have, however, been observed in which the older mycelial branches in rotting tissues swell up and form antheridia and oögonia within these tissues and it is a reasonable assumption that Peronospora-like extinct genera, which perhaps if they could be studied with the facility of existing forms would be referred to extinct families, have existed in past time. I have therefore proposed the generic term *Peronosporoides* for forms like the present which resemble the modern Peronosporaceae and are undoubtedly filiated types.

[9] Felix, J. Zeitz. deutsch. geol. Gesell., 1894, p. 276, pl. 19, fig. 1.

The second form appears to be referable to the genus *Cladosporites* proposed by Felix[9] in 1894 for an Eocene form from Perekeschkul, Austria. It may be called **Cladosporites oligocaenicum** sp. nov. in allusion to its occurrence in wood of lower Oligocene age. It is found in the same rotten stem of *Palmoxylon cellulosum* Knowlton as *Peronosporoides palmi.* It shows a much-branched intra-cellular mycelium with united side branches and made up of fine, much-septate hyphae .0028 mm. in diameter. These hyphae proliferate freely within the cells of the parenchyma and occasionally are observed to send off haustoria to the walls. They frequently show terminal conidia which are in linear pairs, triplets or quadruplets, being generally in pairs or triplets. The conidia are sub-spherical in form and range in diameter from .0035 mm. to .0054 mm. For example, in *Pl. 181, f. 4,* the proximal segment is .00357 mm. × .004 mm.; the middle segment is .0045 mm. × .0054 mm.; and the distal segment is .0036 mm. × .004 mm. Associated with these well marked conidia and borne on hyphae of similar size are the objects shown on *Plate 181, fig. 2, 5, and 8,* which it would seem can best be interpreted as zygosporangia. They are without preserved contents and are not certainly identified with *Cladosporites oligocaenicum. Cladosporites* was named by Felix from its resemblance to the members of the existing genus *Cladosporium* Link, but since the habit of forming chains of conidia is a widespread one in the Fungi and the fossil forms are all endoparasites in the vascular axis of trees, the present species being an intra-cellular parasite, I am not prepared to say that they should be referred to the Didymosporae of the Hyphomycetes (Lindau) or just what their nearest existing relatives should be considered to be. An additional species of *Cladosporites* was recently described by Whitford[10] from the Pliocene Snake Creek beds of Nebraska.

The third new species to which I wish to call attention may be named **Cladosporites fasciculatus** sp. nov. It is found in exceeding abundance in silicified specimens of lauraceous wood from the middle Eocene (Yegua formation of the Claiborne group) of

[10] Whitford, A. C., University Studies, Univ. of Nebraska, vol. 14, 1914, 3 pp., 2 pls.

Texas and is entirely unlike any previously recorded fossil forms. I do not know its botanical affinity and rather than multiply generic terms of unknown botanical value I have preferred to refer this and the preceding species to Felix's genus *Cladosporites,* being influenced in the case of the present species by its resemblance to the existing *Cladosporium herbarum* (Pers.) Link. It may be incompletely described as follows: Mycelium intra-cellular, in the vessels of the secondary wood, attached to the vessel walls by haustoria, and forming small fasciculate apparently unbranched tufts projecting freely in the vessel cavity. The hyphae are thin and the majority are somewhat tapering distad although in some cases they taper proximad. Septa were not observed. In only one case was a distal branch observed (*Pl. 182, f. 1.*) Although there are some hundreds of tufts of this fungus in the slides examined, only two of these show conidia (*Pl. 182, f. 2*). The latter are terminal, fusiform in outline and somewhat variable in length. They appear to be simple and I am unable to assert positively that they are cut off from the hyphae by septa although I imagined that I saw such septation. The hyphae average about .0013 mm. in diameter and the conidia range from .002 mm. × .004 mm. to .002 mm. × .012 mm. in diameter.

Associated with this species are rambling mycelial hyphae which clamber over the vessel walls. These bear numerous antheridia and oögonia or sclerotia and their characteristic appearance is shown in *Pl. 182, f. 2.* I do not consider it worth while to attempt to name or describe them.

The three species that I have ventured to describe are so unique and well preserved as well as so characteristic that I hope their publication may incite some experienced mycologist to delve in the field of fossil fungi which should prove to be a scientifically fruitful as well as delightful occupation.

It has been abundantly proven that we knew but little of the phylogeny of the vascular plants before their extinct ancestors were considered and the same should prove true in the case of the lower plants which are of so much more ancient a lineage.

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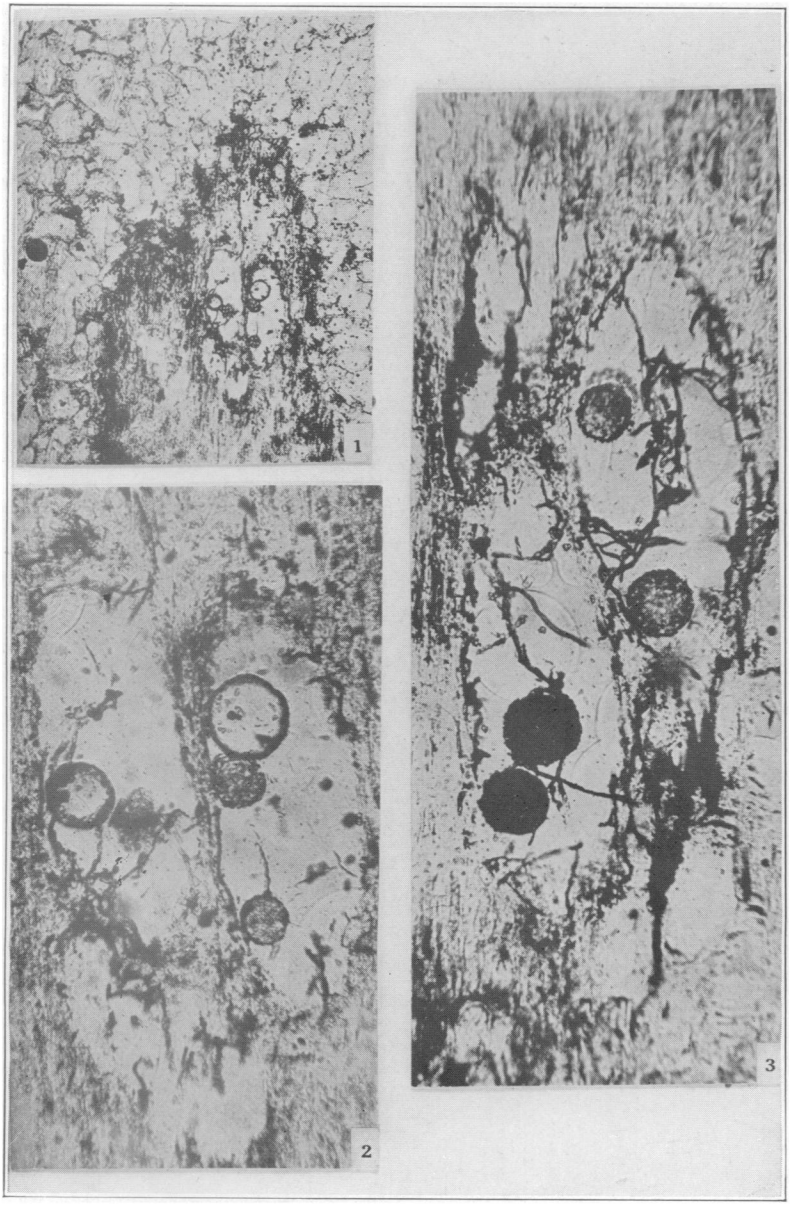
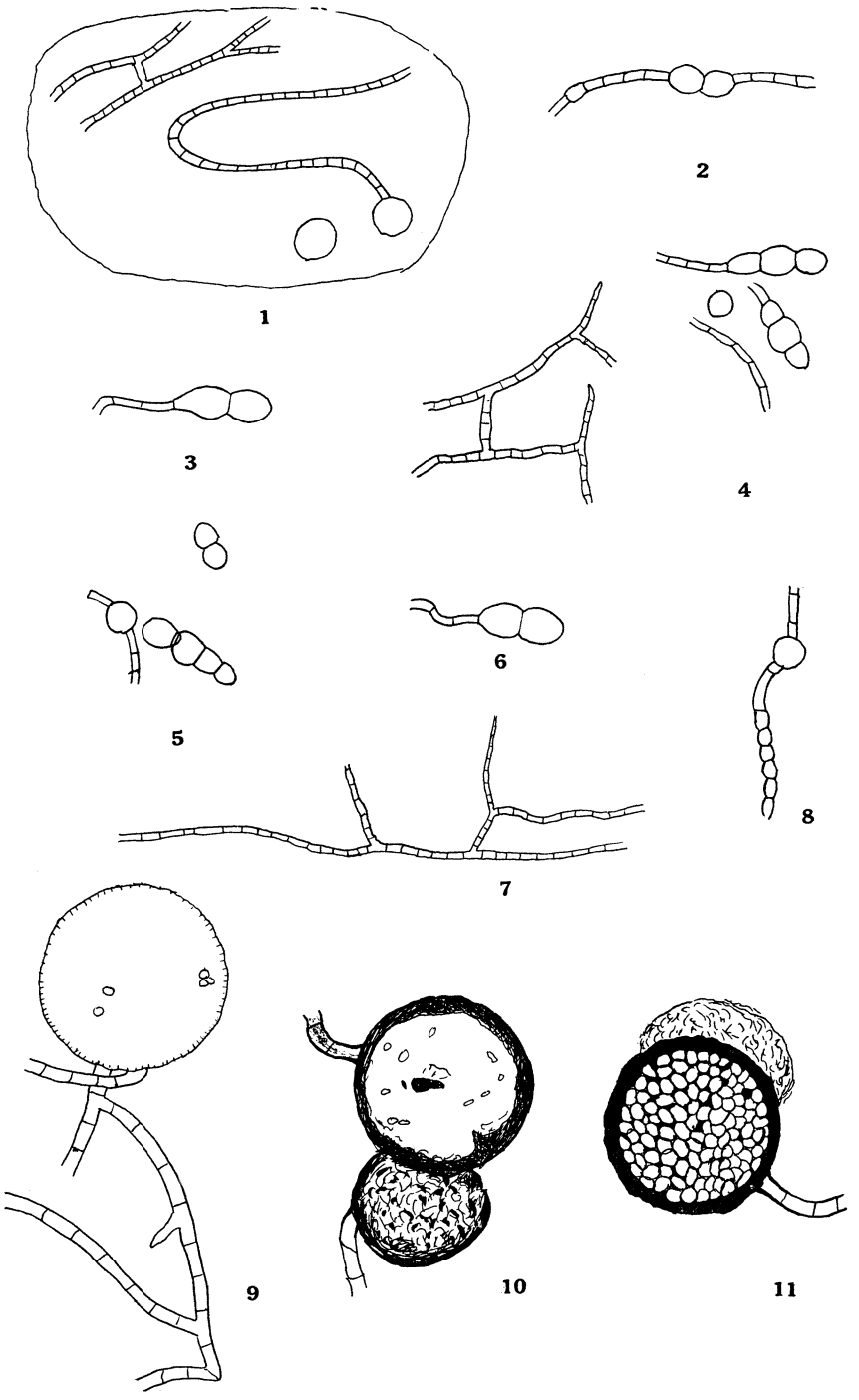
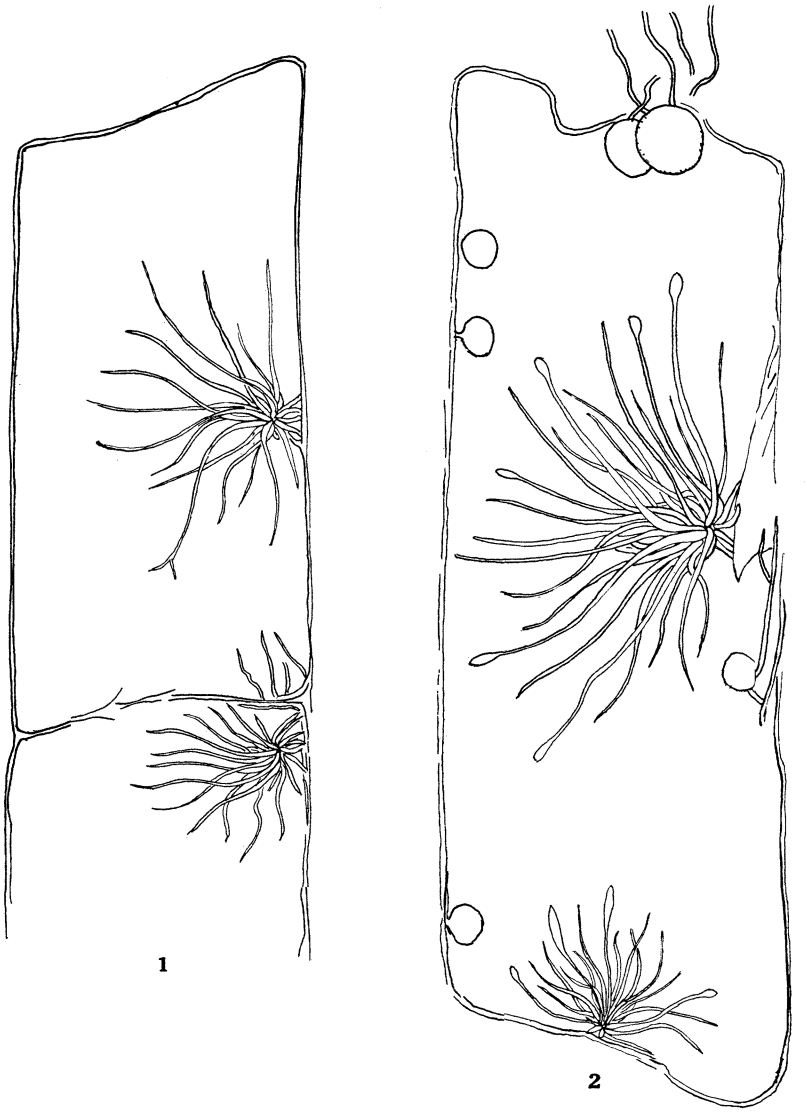


PERONOSPOROIDES PALMI BERRY



1–8. CLADOSPORITES OLIGOCAENICUM BERRY
9–11. PERONOSPOROIDES PALMI BERRY



CLADOSPORITES FASCICULATUS BERRY

EXPLANATION OF PLATES CLXXX–CLXXXII

PLATE CLXXX

Figs. 1–3. *Peronosporoides palmi* Berry. Showing mycelia, antheridia, and oögonia in tissues of *Palmoxylon cellulosum* Knowlton from the lower Oligocene of Bayou Pierre, Mississippi. Fig. 1, × 50; figs. 2 and 3, × 200.

PLATE CLXXXI

Figs. 1–8. *Cladosporites oligocaenicum* Berry. Showing mycelia, zygosporangia, and conidia in the tissues of *Palmoxylon cellullosum* Knowlton from the lower Oligocene of Bayou Pierre, Mississippi. × 400.

Figs. 9–11. *Peronosporoides palmi* Berry.

Fig. 9. Mycelium with oögonium. × 400.

Fig. 10. Antheridium and oögonium. × 400.

Fig. 11. Oögonium with oöspores and traces of collapsed antheridium. × 400.

PLATE CLXXXII

Figs. 1, 2. *Cladosporites fasciculatus* Berry. Showing mycelia and conidia in vessels of *Laurinoxylon* from Middle Eocene of Westmorland Bluff, Trinity River, Texas. × 400